

Evaluation of yield loss in field sorghum from a C₃ and C₄ weed with increasing CO₂

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Dwarf sorghum (C₄) was grown at ambient and at projected levels of atmospheric carbon dioxide (250 mol mol⁻¹ above ambient) with and without the presence of a C₃ weed (velvetleaf) and a C₄ weed (redroot pigweed), to quantify the potential effect of rising atmospheric carbon dioxide concentration [CO₂] on weed–crop interactions and potential crop loss. In a weed-free environment, increased [CO₂] resulted in a significant increase in leaf weight and leaf area of sorghum but no significant effect on seed yield or total aboveground biomass relative to the ambient CO₂ condition. At ambient [CO₂] the presence of velvetleaf had no significant effect on either sorghum seed yield or total aboveground biomass; however, at elevated [CO₂], yield and biomass losses were significant. The additional loss in sorghum yield and biomass was associated with a significant (threefold) increase in velvetleaf biomass in response to increasing [CO₂]. Redroot pigweed at ambient [CO₂] resulted in significant losses in total aboveground biomass of sorghum but not in seed yield. However, as [CO₂] increased, significant losses in both sorghum seed yield and total biomass were observed for sorghum–redroot pigweed competition. Increased [CO₂] was not associated with a significant increase in redroot pigweed biomass ($P = 0.17$). These results indicate potentially greater yield loss in a widely grown C₄ crop from weedy competition as atmospheric [CO₂] increases.

Nomenclature: Dwarf sorghum, *Sorghum bicolor* cv. 'Martin,' redroot pigweed, *Amaranthus retroflexus* L. AMARE; sorghum, *Sorghum bicolor* L. Moench; velvetleaf, *Abutilon theophrasti* Medicus ABUTH.

Key words: Carbon dioxide, climate change, competition, sorghum, yield.

Ongoing increases in atmospheric CO₂ concentration, [CO₂], are now well established, and projected concentrations suggest a doubling of current global values by the end of the 21st century (Keeling and Whorf 2001; Schimel et al. 1996). Although [CO₂]-induced climatic change remains the principal focus of the scientific community, the continuous increase in atmospheric [CO₂] may alter agricultural productivity per se by differentially affecting the physiology, biochemistry, and growth of crops and weeds (for reviews see Patterson 1993; Patterson and Flint 1990).

If differential responses to increasing [CO₂] occur between crops and weeds, will crop losses due to weedy competition increase or decrease? Early, subjective classification of weeds by Holm et al. (1977) indicated that a majority (14 of 18) of the world's "worst" weeds were C₄, whereas of the 86 crop species that make up 96% of the world's food supply, only five are C₄ (Patterson 1995). Because the C₄ photosynthetic pathway is overrepresented among weedy species, initial experiments analyzed C₃ crop–C₄ weed competition (e.g., Alberto et al. 1996; Carter and Peterson 1983; Patterson et al. 1984). These studies uniformly reported that increasing [CO₂] resulted in a greater ratio of crop to weed vegetative biomass (i.e., C₃:C₄), which is consistent with the known carboxylation kinetics of the C₃ and C₄ pathways (Bowes 1996). Hence, many global models have indicated less crop loss due to weedy competition as atmospheric [CO₂] increases (see Rosenzweig and Hillel 1998, chapter 4).

However, such an interpretation represents a gross oversimplification. For example, it also can be stated that four

of the top 10 producing crops globally are C₄ (corn, *Zea mays* L.; millet, *Panicum miliaceum* L.; sorghum; and sugarcane, *Saccharum officinarum* L.) and that of the 33 most invasive weeds globally (which can certainly be considered among the worst weeds categorically), only two are C₄ (common cordgrass [*Spartina anglica*] and cogon grass [*Imperata cylindrica* (L.) Beauv.]) (www.issg.org/database). In addition, a C₃ crop vs. C₄ weed interpretation does not address weed–crop interactions where the photosynthetic pathway is the same. Yet, many of the most troublesome weeds for a given crop are genetically similar and frequently possess the same photosynthetic pathway (e.g., sorghum and johnsongrass, *Sorghum halepense* (L.) Pers, both C₄; oat, *Avena sativa* L., and wild oat, *Avena fatua* L., both C₃).

Preliminary data from all known studies on the response of C₃ crops and weeds grown concurrently indicated that the vegetative growth of the weed was favored over that of the crop (see Bunce and Ziska 2000, table 15.4). For the single study examining a C₄ crop and a C₃ weed, elevated [CO₂] increased the vegetative biomass of cocklebur (*Xanthium strumarium* L.) relative to that of sorghum (Ziska 2001).

However, CO₂-induced changes in biomass do not necessarily reflect changes in potential yield. Only a single investigation to date has quantified the actual change in yield loss from weedy competition at elevated [CO₂] under field conditions (Ziska 2000). In this instance, soybean (C₃) [*Glycine max* (L.) Merr.] was grown at ambient and ambient + 250 mol mol⁻¹ (elevated) [CO₂] with and without the presence of two weeds, lambsquarters [*Chenopodium album* (L.)]

(C₃) and redroot pigweed (C₄), at a density of two weeds per meter of row. If lambsquarters was present, the reduction in soybean seed yield relative to the weed-free condition increased from 28 to 39% with elevated [CO₂]. For redroot pigweed, soybean seed yield losses diminished with elevated [CO₂] from 45 to 30%.

The soybean study strongly suggested that the ongoing increase in atmospheric [CO₂] may have important consequences for weed-crop competition and subsequent economic losses. However, at present, no data are available quantifying similar yield losses associated with weedy growth for C₄ crops. Consequently, in the current experiment, the principle objective was to test whether increased atmospheric [CO₂] would alter current vegetative and reproductive losses due to competition with a C₃ and C₄ weed, using grain sorghum, a common C₄ crop, as a test case.

Materials and Methods

Dwarf sorghum was grown in 12 open-top chambers located in a field plot at Beltsville, MD. Field soil is classified as a Codruss silt-loam with pH 5.5 and high availability of potash, phosphate, and nitrate (*Codruss hatboro*). Experimental chambers consisting of a cylindrical aluminum frame (3 m in diameter and 2.25 m in height) that covered an area of 7.2 m² were constructed before the experiment. Because of the size of the chambers, a modified suspended chamber top was necessary to prevent wind intrusion and to maintain a stable CO₂ concentration. Each chamber was assigned one of two [CO₂] treatments (ambient or ambient + 250 mol mol⁻¹). [CO₂] treatments were maintained 24 h d⁻¹ from germination until maturity. Air was supplied through perforations in the lower plenum within the chamber. Air was adjusted to the proper [CO₂], with pure CO₂ supplied from a liquid CO₂ tank. Gas samples from a given chamber were drawn at 4-min intervals at canopy height, and adjustments to [CO₂] for the elevated chambers were made daily. [CO₂] was determined with an absolute CO₂ analyzer.¹ [CO₂] values indicated an average daytime [CO₂] (6:00 A.M. to 7:00 P.M.) of 392 ± 12.1 mol mol⁻¹ and 616 ± 13.3 mol mol⁻¹ and an average nighttime [CO₂] of 536 ± 20.7 mol mol⁻¹ and 755 ± 21.0 mol mol⁻¹ for the ambient and elevated treatments, respectively. Micrometeorological conditions of photosynthetic photon flux and air temperature indicated that the chamber transmitted 86% of incoming light, with an average daytime temperature increase of 1.4 °C relative to the outside environment.

Soil was tilled on June 4, 2002, and sorghum was planted on June 6, 2002. Row widths were approximately 40 cm within chambers and for border rows outside chambers. Three outside experimental plots of the approximate area of the chamber also were planted to compare chamber-induced micrometeorological effects. All sorghum seedlings were thinned to one plant per 10 cm of row after emergence. Seed of either velvetleaf (C₃) or redroot pigweed (C₄) obtained from local populations were sown simultaneously with sorghum (but at a slightly shallower depth) for one-half of each experimental chamber. After emergence, these weeds were thinned to a density of two weeds per meter of row. Emerged weed seedlings were marked with plastic stakes, and all other weeds that emerged during the experiment were removed by hand at weekly intervals from all

experimental plots until 100% crop cover. Each of the 12 experimental chambers was split in a north-south direction into either a weed-free or a plus-weed condition. Sorghum and weeds were arranged in four pairs, sorghum without redroot pigweed (control), sorghum with redroot pigweed, sorghum without velvetleaf (control), and sorghum with velvetleaf among the 24 split plots (i.e., four pairs by three replications by 2[CO₂]) in a completely randomized design. Chambers were watered as needed to match estimates of evapotranspiration. A weather station at the site recorded standard meteorological variables for comparison with chamber values.

Flowering began in the week of July 15th, with no observable difference in time to flowering between treatments. Plants were considered mature when > 95% of seed heads were noticeably brown. Maturity occurred by the week of September 23rd and did not differ as a function of treatment. At maturity, one linear meter of row from each of the two center rows (i.e., excluding border rows) for both the weed-free and the plus-weed plots was cut at the plant base and harvested. Just before cutting, leaf area and dry weight for a sorghum subsample of 10 to 20 leaves from each treatment were determined. All aboveground plant parts were air dried at 65 °C for at least 72 h or until a constant dry weight was maintained. Estimates of leaf area for each row were estimated from the correlation between area and dry weight observed for the subsample ($r^2 > 0.89$ in all cases). After drying, seed heads were threshed, seed collected, and the ratio of seed to panicle weight determined. Concurrently with single-row harvests of plus-weed sorghum, weeds (either redroot pigweed or velvetleaf) were cut at ground level, dried at 65 °C, and weighed. Individual seed pods of velvetleaf also were recorded at that time.

Aboveground biomass at maturity of sorghum and weeds and seed yield and yield parameters of sorghum were analyzed using a one-way analysis of variance (Statview,² SAS, NC) to determine the effect of [CO₂] on sorghum under a weed-free condition and to determine the effect of [CO₂] on a given weed-sorghum interaction. Unless otherwise stated, all differences compared with the ambient or elevated [CO₂] weed-free condition are significant at the 0.05 level.

Results and Discussion

Under a weed-free condition, increasing the [CO₂] by 250 μmol mol⁻¹ significantly increased sorghum leaf biomass and area; however, no concurrent change in seed yield or aboveground biomass was observed. Consequently, harvest index was significantly reduced (Table 1). Comparisons of sorghum grown at ambient conditions within and outside the experimental chambers did not indicate significant differences in any measured growth parameter, suggesting that any microclimatic effect of the chambers was minimal.

For sorghum grown under a weed-free condition, the lack of response of either total biomass or seed yield to enhanced [CO₂] is consistent with previous reports showing that sorghum was not affected by [CO₂] under well-watered conditions (Ellis et al. 1995; Marc and Gifford 1984; Ottman et al. 2001). Interestingly, recent field studies of sorghum grown under free-air CO₂ enrichment (FACE) showed a decline in harvest index with elevated [CO₂] similar to that observed in the current study (Ottman et al. 2001). This

TABLE 1. Dry weight of harvested plant components and reproductive parameters of dwarf sorghum (cv. "Martin") grown under a weed-free condition at ambient and elevated ($+250 \mu\text{mol mol}^{-1}$ above ambient) concentrations of carbon dioxide, $[\text{CO}_2]$. "Outside" refers to non chambered plots. Except for 50 seed weight, all data are given per meter of row (approximately 40-cm row widths).

Treatment $[\text{CO}_2]$	Leaf area	Leaf weight	Stem weight	Seed yield	Total biomass	HI	50 Seed weight
		g m					g
Outside Ambient		147.2	169.6	301.9	638.0	0.50	1.46
Chamber Ambient		139.4	179.6	321.8	664.6	0.48	1.36
Chamber Elevated		163.0*	202.8	302.2	680.6	0.44*	1.29

* Indicates a significant increase relative to the ambient $[\text{CO}_2]$ -chambered condition (one-way analysis of variance). No differences were observed between outside ambient and chamber ambient conditions, indicating that micro climate did not affect potential yield of sorghum. HI is harvest index, determined as seed weight divided by total aboveground dry weight.

suggests a greater response of vegetative characteristics relative to reproductive characteristics in sorghum as $[\text{CO}_2]$ increases, even if total biomass or seed yield are unaffected.

Previous data for sorghum (and for almost all other crops) quantifying the response of yield to changing $[\text{CO}_2]$ have, for the most part, been obtained from single plants or from plants grown in monoculture. Consequently, they do not necessarily reflect in situ agronomic environments in which crops compete with weeds for light, nutrients, water, etc. Agronomic weed assessments of grain sorghum production for the United States indicate that velvetleaf is considered a troublesome weed in the Midwest (Nebraska, Illinois), whereas redroot pigweed is considered a troublesome weed in the South (Alabama, Georgia) (Bridges 1992). In agronomic practice, "troublesome" usually refers to a weed that consistently affects production quantity or quality.

At the ambient $[\text{CO}_2]$ condition, the presence of redroot pigweed resulted in a significant reduction in total biomass but not in grain yield of sorghum, whereas no significant effect of velvetleaf on sorghum growth was observed (Figure 1). In contrast, at elevated $[\text{CO}_2]$, significant reductions in both sorghum yield and biomass were observed for velvetleaf

(-16 and -14% , respectively) and redroot pigweed (-23 and -20% , respectively) relative to the elevated $[\text{CO}_2]$, weed-free condition (Figure 1). The increase in $[\text{CO}_2]$ was associated with a threefold increase in aboveground biomass of velvetleaf and a slight, but nonsignificant ($P = 0.17$), increase in the aboveground biomass of redroot pigweed (Figure 2). Seed shattering prevented any estimate of reproductive effort for redroot pigweed; however, the average number of seed pods per velvetleaf plant approximately doubled (6.1 to 11.5) at the higher $[\text{CO}_2]$ (data not shown).

Among growth and reproductive parameters of sorghum, no effect of velvetleaf was observed at ambient $[\text{CO}_2]$, whereas at elevated $[\text{CO}_2]$ significant reductions in leaf area, leaf weight, and average seed weight were noted (Table 2). The decline in total biomass for sorghum grown with redroot pigweed at ambient $[\text{CO}_2]$ was primarily associated with a reduction in leaf area and weight (Table 2). However, at elevated $[\text{CO}_2]$, significant reductions in leaf area and weight, as well as in average seed weight, were observed for sorghum when grown with redroot pigweed. The presence of either weed had no effect on harvest index at any treatment $[\text{CO}_2]$.

For the current experiment, it was clear that under ambient conditions, redroot pigweed was a much more effective competitor than velvetleaf. Conversely, at the higher $[\text{CO}_2]$, weedy competition, as determined from changes in sorghum seed yield, increased significantly for both weed species. The resulting decline in sorghum seed yield at the higher $[\text{CO}_2]$ was associated with a concomitant increase in velvetleaf bio-

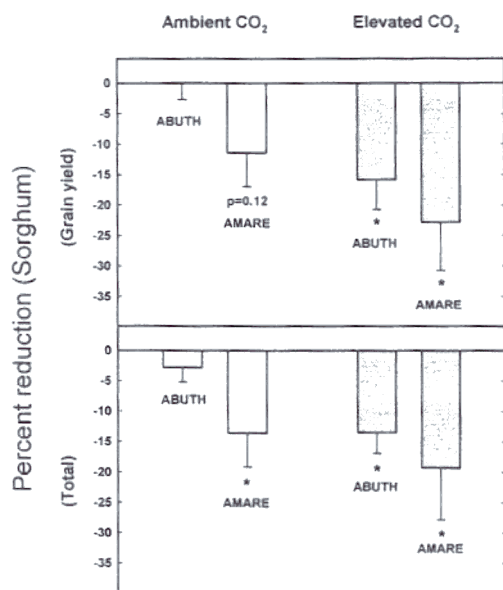


FIGURE 1. Percent reduction in sorghum grain yield or biomass at maturity (per-meter of row) when grown with either a C_3 weed (velvetleaf) or a C_4 weed (redroot pigweed) at either ambient or elevated (ambient $+250 \mu\text{mol mol}^{-1}$) concentrations of carbon dioxide. Weed density was two plants per meter of row. * indicates a significant difference relative to the weed-free condition (one-way analysis of variance). Bars are \pm SE.

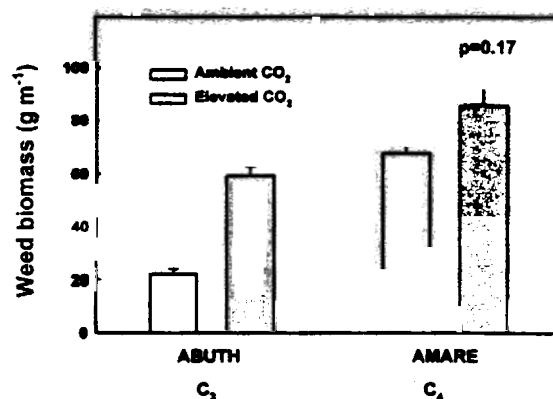


FIGURE 2. Above-ground weed biomass (per meter of row) for a C_3 weed (velvetleaf) or a C_4 weed (redroot pigweed) grown at either ambient or elevated (ambient $+250 \mu\text{mol mol}^{-1}$) concentrations of carbon dioxide. * indicates a significant increase in biomass relative to the ambient $[\text{CO}_2]$ treatment (one-way analysis of variance). Bars are \pm SE.

TABLE 2. Dry weight of harvested plant components and reproductive parameters of dwarf sorghum (cv. "Martin") grown with and without weedy competition at ambient and elevated (250 $\mu\text{mol mol}^{-1}$ above ambient) concentrations of carbon dioxide, $[\text{CO}_2]$. The C_3 and C_4 weeds were velvetleaf and redroot pigweed, respectively. Except for 50 seed weight, all data are given per meter of row (approximately 40-cm row widths).

Treatment	Leaf area	Leaf weight	Stem weight	50 Seed weight	Seed: panicle	HI
		g m		g		
Ambient [CO ₂]						
Sorghum, weed-free	2.47	138.3	178.7	1.30	0.93	0.53
Sorghum, velvetleaf	2.25	126.6	164.0	1.28	0.94	0.54
Sorghum, weed-free	2.54	142.7	174.3	1.31	0.93	0.50
Sorghum, pigweed	2.09 ^a	117.3 ^a	157.0	1.41	0.96	0.50
Elevated [CO ₂]						
Sorghum, weed-free	3.66	156.8	203.2	1.29	0.95	0.45
Sorghum, velvetleaf	2.97 ^a	127.3 ^a	174.6	0.85 ^a	0.91	0.45
Sorghum, weed-free	3.86	165.3	202.3	1.29	0.95	0.48
Sorghum, pigweed	3.05 ^a	130.7 ^a	174.0	1.18 ^a	0.96	0.46

^a Indicates a significant difference for a given weed-sorghum combination relative to the weed-free condition at a given $[\text{CO}_2]$ (one-way analysis of variance). HI is harvest index, determined as seed weight divided by total aboveground dry weight; seed:panicle is the ratio of seed to total panicle weight.

mass and pod production. Because of the difficulty in separating root biomass between species, it is impossible to determine whether the greater reduction in sorghum yield from weeds at the higher $[\text{CO}_2]$ was a consequence of greater competition for light, for nutrients, or for both. Separation and quantification of specific yield or growth limitations due to aboveground (e.g., light) or belowground (e.g., nutrients, water) weedy competition in a field situation is extremely difficult (see Patterson and Flint 1990). However, the stimulation of velvetleaf biomass observed here is consistent with that of lambsquarters exposed to elevated $[\text{CO}_2]$ (ca. 250 mol mol^{-1} above ambient) in field-grown soybean (Ziska 2000).

The current field data obtained for sorghum and those obtained previously for soybean (using the same field and treatment $[\text{CO}_2]$, see Ziska 2000), suggest that crop yield loss associated with weedy competition is reduced only in a C_3 crop- C_4 weed association as $[\text{CO}_2]$ increases. In all other crop-weed associations (i.e., C_3 crop and C_3 weed, C_4 crop with either C_4 or C_3 weed), crop yield loss is exacerbated with increasing $[\text{CO}_2]$. The current data on sorghum yield loss with the C_3 weed velvetleaf are consistent with those on vegetative response of sorghum when grown concurrently with the C_3 weed cocklebur (Ziska 2001). Overall, the data presented here and those of previous studies (e.g., Ziska 2000) reinforce the suggestion of Treharne (1989) that the physiological plasticity and greater genetic diversity of weed species relative to modern crops would provide a greater competitive advantage as atmospheric $[\text{CO}_2]$ increases.

Even if seed yield loss due to weedy competition increases in a future, higher- $[\text{CO}_2]$ environment, is this a cause for concern? It can be argued that use of genetically modified organisms that allow blanket application of herbicides would negate any potential change in the weed-crop ratio in response to $[\text{CO}_2]$. However, there are an increasing number of studies that demonstrate that herbicide efficacy is reduced in response to increasing $[\text{CO}_2]$ (Ziska and Teasdale 2000; Ziska et al. 1999). This would suggest that herbicide use, per se, may not negate the differential response of weeds and the resulting changes in crop yield loss as atmospheric $[\text{CO}_2]$ increases.

Given the importance of weed-crop interactions, it is unclear why so few data are available that assess the effect of rising atmospheric $[\text{CO}_2]$ on potential crop yield. The argument that rising $[\text{CO}_2]$ will reduce weedy competition because the C_4 photosynthetic pathway is overrepresented among the worst weeds is clearly not applicable to all weed-crop interactions in an agronomic setting. In reality, there are few agronomic situations where a C_3 crop competes exclusively with C_4 weeds (see Bunce and Ziska 2000, table 15.2). Rather, competition occurs against an assemblage of C_3 and C_4 weeds, with the worst weeds having a similar form or function, or both, as the associated crop species (Patterson and Flint 1990).

The initial results presented here and those reported previously (Ziska 2000) indicate $[\text{CO}_2]$ -induced changes in weed-crop competition and subsequent crop production. They also illustrate a critical need for additional field data on multiple crop-weed comparisons over a range of $[\text{CO}_2]$ to assess more accurately competition, weed population biology, weed-induced yield losses, and agricultural productivity. Clearly, our current understanding regarding the effect of rising $[\text{CO}_2]$ with respect to weed establishment, growth, reproduction, and competition is limited. Yet, the environmental and economic costs of not understanding these effects and the appropriate control measures to ameliorate them may be substantial.

Sources of Materials

¹ CO_2 analyzer, Li-Cor, model 6252, Li-Cor Corporation, 4421 Superior Street, Lincoln, NE 68504.

² Starview, Version 5, SAS Institute Inc., SAS Campus Drive, Cary, NC 27513-2414.

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